

THE ORIGIN AND HOMOLOGIES OF THE SO-CALLED  
"SUPERLINGUÆ" OR "PARAGLOSSÆ" (PARAGNATHS)  
OF INSECTS AND RELATED ARTHROPODS.

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In several recent papers published in the Fiftieth Report of the Entomological Society of Ontario, the Transactions of the Entomological Society of London, and the Annals of the Entomological Society of America, I have called attention to many current misinterpretations of the homologies of various structures in insects; but since no figures were there given, in which the parts of insects were compared with those of Crustacea and allied arthropods, I would present the following brief consideration of the comparative anatomy of the paragnaths (or "superlinguæ") in insects, Crustacea, etc., as the second of a series of papers dealing with the comparative morphology of insects and their arthropodan relatives, from the standpoint of evolution (the first paper of the series, which deals with the evolution of the mandibles, has recently been published in the Journal of the New York Entomological Society).

During the course of these investigations, it has been a source of continual amazement to me that such patently impossible, and obviously untenable views concerning the interpretation of the mouthparts of insects, as are now current among entomologists, could have gained such universal acceptance in these days of scientific progress, when abundant, and easily-examined material, illustrating the true interpretation of the parts so clearly that the veriest tyro could not mistake them, is available to anyone with enterprise enough to capture a common mayfly naiad (nymph) from the nearest stony brook, and compare it with any common *Asellus* from the nearest pond! That this statement is not exaggerated may be seen, for example, when one compares the much-misunderstood "superlinguæ," "paraglossæ," or "maxillulæ" of an insect, such as the common mayfly naiad shown in Fig. 2 (Plate V), with the corresponding parts in one of the common *Ligyda exotica* (Fig. 1) from the Carolina coast. The ubiquitous *Asellus*

*communis*, found in almost any pond, would have served equally well for the purpose of comparing the "superlinguæ" (paragnaths) in the two groups of arthropods, but *Ligyda* has a large median lobe, or lingua, which is not developed in *Asellus*, thus making it somewhat easier to compare all of the parts under consideration, in the two groups of arthropods (insects and Crustacea), and on this account, *Ligyda*, rather than *Asellus* is here used for the purpose of comparison.

If the underlip and maxillæ of the mayfly naiad are removed, as in Fig. 2, one may readily observe immediately behind, and between, the mandibles "md", a structure called the *hypopharynx*, which is composed of a median, tongue-like lobe, the *lingua*, "li", and a pair of lateral lobes, "pg", which the entomologists call "superlinguæ", or "paraglossæ" (a term which should be restricted to the outer lobes on either side of the glossæ of the labium). Similarly, in the crustacean shown in Fig. 1, if the underlip and the two pairs of maxillæ are removed, one may observe immediately behind, and between, the mandibles, "md", a hypopharynx (exactly like that of the mayfly shown in Fig. 2) composed of a median, tongue-like lingua, "li", and a pair of lateral lobes, "pg", which the carcinologists call *paragnaths*. In the following discussion, I have applied the carcinologists' term paragnaths, to the corresponding structures in insects, and I have applied the entomologists' terms lingua and hypopharynx to the corresponding structures in Crustacea, and allied arthropods.

The absolutely patent correspondence between the parts of the hypopharynx of an insect (Fig. 2), and a crustacean (Fig. 1), which is so simple and utterly obvious, that it should be evident to anyone possessed of even the rudiments of a knowledge of comparative anatomy, has apparently suffered through its very obviousness and simplicity, for the human mind is apt to regard the obvious with suspicion, as though it were a snare to entrap the careless or indiscriminating observer, and to seek for subtler analogies which appeal more strongly to the imagination, and stimulate the speculative faculties. The unmistakable resemblance between the hypopharynx of an insect (Fig. 2) and that of a crustacean (Fig. 1), however, is not merely a superficial re-

semblance calculated to deceive the unwary, since the hypopharynx in the two groups not only occupies the same position, and has the same form and structure in both insects and Crustacea, but it also has exactly the same embryological development, and serves the same function (i. e., that of a secondary underlip, provided with taste organs, etc.) in both groups—and what more could one ask, to establish complete homology? I would therefore maintain that the so-called “superlinguæ” of insects do *not* represent the maxillulæ or first maxillæ of Crustacea, since they do not occupy exactly the same position, they do not exhibit the same form and structure, they do not have exactly the same embryological development, and they do not have exactly the same function in the two groups; and I would claim that the so-called “superlinguæ” of insects most emphatically do represent the paragnaths of Crustacea, since they agree with these in all of the features mentioned above.

Since the “superlinguæ” of insects represent the paragnaths of Crustacea, by comparing the higher Crustacea, which are near insects, with the lower Crustacea, which approach the trilobites and other primitive arthropods, we are able to trace the evolution of these structures, and to determine their morphological significance. In *Ligyda* (Fig. 1) the paragnaths, “pg”, are rather closely associated with the median lingua, “li”, which appears to be formed as a projection of the pharyngeal ridge, “pc”, behind it, which apparently includes in its composition a portion of the sterna of certain of the mouthpart segments. In *Talorchestia* (Fig. 3) the lingua, “li”, is represented by a double ridge, or lobe-like projection of the median pharyngeal ridge, “pc”; and it would appear that the median, basal portions of the paragnaths, “pg”, likewise take part in the formation of the lingua, “li”, so that the lingua of higher Crustacea and insects may be formed in part by the paragnaths, although the greater part of the lingua is probably formed by portions of the sterna of certain of the mouthpart segments, as is indicated by embryology. On either side of the median pharyngeal ridge, “pc”, of Figs. 1 and 3, are rib-like structures, “te”, which are located at the base of the trophi or mouthparts. It is possible that the lingual loræ, “ll”, of Figs. 2 and 8, represent

modifications of these rib-like or ridge-like structures in insects, and it is also possible that certain of these structures may be the precursors of portions of the tentorium of insects, although I have not been able to determine this point as yet.

The pharyngeal ridge, "pc", of Fig. 3, etc., appears to represent a portion of the sterna of the mouthpart segments, which are quite broad in Fig. 4; and the lingua is not developed in the lower Crustacea. In *Mysis* (Fig. 4) the paragnaths, "pg", are borne at the anterior margin of the sternite, "mxs", of the first maxillary segment; and in the lower Crustacea, the paragnaths appear to be more closely associated with the maxillulæ or first maxillæ, than they are with the mandibles, thus indicating that the paragnaths may represent detached lobes of the first maxillæ.

In *Squilla* (Fig. 6), the paragnaths, "pg", are attached to the basal portions of the maxillulæ or first maxillæ, "mx", and in the very primitive crustacean *Apus* (Fig. 7) both paragnaths, "pg", and maxillulæ, "mx", arise from the same basal lamina, "bl", which projects internally beneath the body wall. The paragnaths and maxillulæ in Fig. 7 are bent over backward (instead of being represented in their normal upright position, as in Fig. 6), in order to show that both paragnaths and maxillulæ are borne on the same basal lamina. The fact that both paragnaths and maxillulæ arise from the same basal lamina in such primitive forms as *Apus*, would indicate that the paragnaths of higher Crustacea are merely detached lobes of the maxillulæ, possibly corresponding to the endites or gnathobase-like structures of the trunk limbs of *Apus*; and in the higher Crustacea, these paragnathal lobes become more or less separated from the remainder of the first maxillæ (maxillulæ), and become somewhat more closely associated with the mandibles, as a secondary modification.

I do not know of any instance in which the paragnaths are situated in front of the mandibles, so that the metastoma, "mts", of the trilobite *Triarthrus* (Fig. 10), which is situated in front of the bases of the so-called mandibular appendages, "md", (only the tips of the basal segments of these are shown in the figure) and occupies a position between the bases of the so-called second antennæ, "at", is situated too far forward in the head region, to

occupy a position strictly comparable to that of the paragnaths, unless it be true that the so-called second antennæ of trilobites, are in reality the representatives of the mandibular appendages of other arthropods. In certain trilobites there is a rather deep median incision, or emargination in the metastoma, thus suggesting that this organ may have been formed by the union of two lobes like the paragnaths; but this cannot be demonstrated from the material at present available. The suggestion that the metastoma of trilobites may represent the united paragnathal lobes of Crustacea, is thus merely a speculation, and has no particular bearing upon the subject of the origin and development of the paragnaths in Crustacea and insects.

I imagine that there are still some individuals who will vigorously maintain that the "superlinguæ" of insects must represent the maxillulæ (first maxillæ) of Crustacea, on the ground that Folsom, 1900, has described in a collembolan embryo a supposed "superlingual" segment, or neuromere, which he claims is the representative of the first maxillary segment of Crustacea; and he further claims that since the "superlinguæ" are supposedly the appendages of this alleged "superlingual" segment, they must therefore represent the maxillulæ, or appendages of the corresponding first maxillary segment, in Crustacea.

In reply to this argument, it is sufficient merely to call attention to the fact that Philiptschenko, 1912 (*Zeitschr. Wiss. Zoologie*, Bd. CIII), who has made an exceptionally careful and thorough study of collembolan embryology, and has attempted to verify Folsom's work on these insects (*Bull. Harvard Mus. Comp. Zoology*, 1900, Vol. 36, No. 5), has demonstrated that the supposed "superlingual" neuromere, or embryonic segment, described by Folsom, exists only in its author's imagination; and recent writers who quote Folsom's mistaken observations as though they were established facts, are apparently wholly ignorant of Philiptschenko's work, and know even less of the anatomy and embryological development of the structures of Crustacea with which they seek to compare the structure of insects. If there were no other reasons for discrediting the statement that the "superlinguæ" represent the maxillulæ of Crustacea, the fact that the *paragnaths* (*not* the

maxillulæ) of Crustacea develop embryologically in exactly the same position and in the same way as the "superlinguæ" do in the embryos of insects, would be sufficient to completely disprove this unfounded and misleading statement, and it is hardly in keeping with the modern scientific spirit to continue to promulgate such misinformation, when a little time spent in the reading of the literature of the subject, or in easily conducted research, would readily convince anyone of its falsity.

Carpenter, 1903 (Proc. Royal Irish Academy, Vol. 24, Section "B", Part 4), interprets the structures labeled "a", "b", and "c", in Fig. 9, of the paragnath of *Machilis maritima*, as the representatives of the lacinia, galea, and palpus of the first maxilla (or "maxillula") of a crustacean, in an effort to prove that the "superlinguæ" (paragnaths) of insects represent the maxillulæ of Crustacea. The structures which he figures in the "superlingua" of *Machilis*, however, are nothing like the true lacinia, galea, and palpus of the maxillulæ themselves, in Crustacea, but are exactly like similar structures found in the paragnaths of Crustacea, as one would expect to be the case if the "superlinguæ" of *Machilis* represent the paragnaths, not the maxillulæ, of Crustacea. Literally hundreds of Crustacea exhibit in their paragnaths small projections like those labeled "a" and "b" in Fig. 9; and these projections of the paragnaths of Crustacea not only have the same appearance as these structures in the "superlingua" of *Machilis*, but they also bear the same type of hairs, taste organs, etc., as in *Machilis*. Furthermore (as I have pointed out in several papers), the palpus of a maxilla of an insect, or crustacean, represents the terminal segments of a mouthpart limb (the endopodite) in which the basal segments form the body of the maxilla, the galea and lacinia being appendages (endites, or gnathobase-like structures) of the basal segments of the maxillary limb. Since the palpus represents the terminal segments of such a modified limb, and since the "superlinguæ" (paragnaths) do not represent modified limbs, they cannot possibly have a palpus; and the small outgrowth labeled "c" in Fig. 9 of the paragnath ("superlingua") of *Machilis*, is merely a small, secondarily formed appendage, similar in nature to the articulated appendage "c", borne on the paragnath of the



crustacean shown in Fig. 5. In Fig. 14, Plate II, of a paper on *Anurida* (L.M. B. C. Memoir No. XIII), an appendage of this kind, borne near the tip of the paragnaths as in *Apseudes* (Fig. 5), is figured in the "maxillulæ" (i. e. the true paragnaths) of the insect *Anurida*, by Imms, 1906; and in both insects and Crustacea, these appendages of the paragnaths cannot possibly be homologized with the palpus, or terminal segments of the endopodite of the limb forming the maxillula, or first maxilla.

The principal points brought out in the foregoing discussion may be briefly summarized as follows. The great similarity between the hypopharynx of insects and Crustacea lends additional weight to the evidence of a very close relationship between these two groups of arthropods, furnished by a study of numerous other structures of the body as well; and since no such close correspondence in the details of the parts of insects and chilopods exists, it is infinitely more probable that insects were descended from crustacean-like (instead of chilopod-like) ancestors. The "superlinguæ" of insects are completely homologous with the paragnaths of Crustacea, because they occupy exactly the same position, and have the same form, structure, and function in the adult condition, and arise in the same location, and in the same fashion, during embryonic development in both groups of arthropods, thus fulfilling all the requirements for establishing complete homology between the corresponding parts in insects and Crustacea. Since the paragnaths of Crustacea are not the maxillulæ of Crustacea, it is folly to state that the "superlinguæ" of insects correspond to the maxillulæ of Crustacea, if they represent the paragnaths of Crustacea instead; and it is to be hoped that if anyone is unwilling or unable to inform himself as to the truth in this matter, that he will at least refrain from deceiving others by promulgating the misinformation that the "superlinguæ" of insects represent the maxillulæ of Crustacea, as though it were a demonstrated fact!

#### EXPLANATION OF PLATE V.

Fig. 1. Posterior (ventral) view of mandibles and hypopharynx of the crustacean *Ligyda*.

Fig. 2. Same of a nymph of the mayfly *Heptagenia*. The hypoporus, or salivary pore beneath the hypopharynx is not shown.

Fig. 3. Posterior (ventral) view of the hypopharynx of the crustacean *Talorchestia*.

Fig. 4. Ventral (posterior) view of the sternum of the first maxillary segment, and the paragnaths of the crustacean *Mysis*.

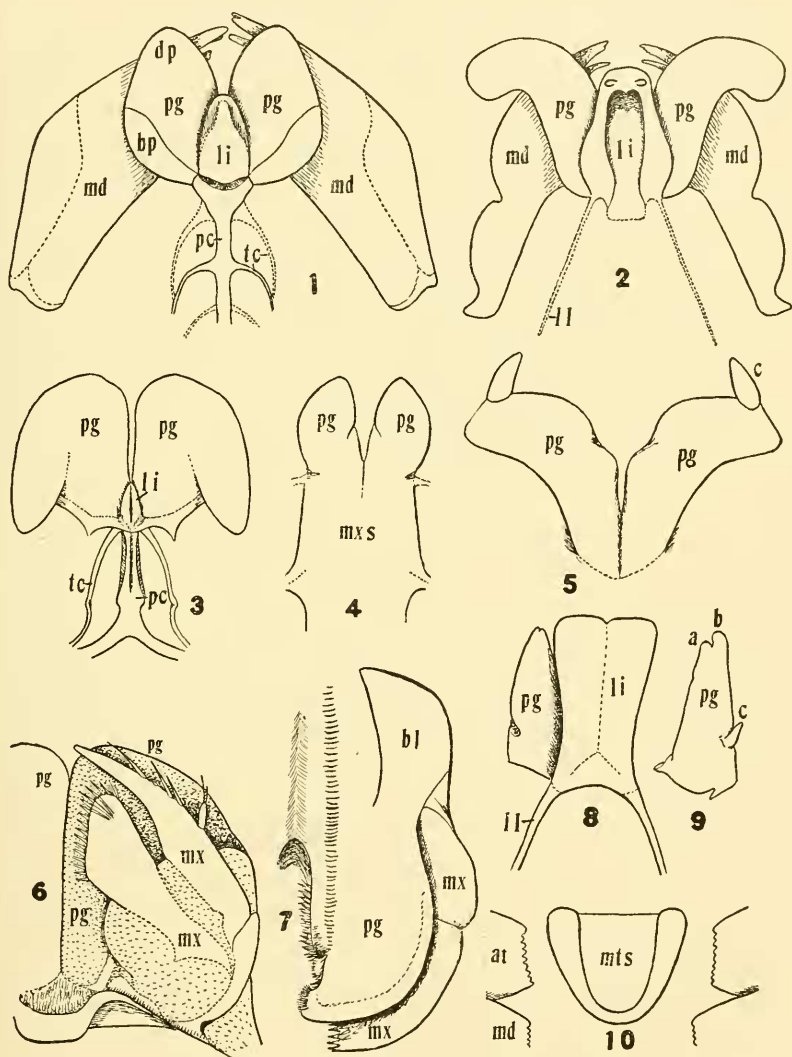




Fig. 5. Posterior (ventral) view of the paragnaths of the crustacean *Apseudes*.

Fig. 6. Posterior (ventral) view of a paragnath and maxillula of the crustacean *Squilla*.

Fig. 7. Anterior (dorsal) view of a paragnath and maxillula of the crustacean *Apus*, bent over backward to show attachment to the basal lamina.

Fig. 8. Ventral (posterior) view of a paragnath and the lingua of the insect *Machilis*.

Fig. 9. Same view of a paragnath of *Machilis* taken from a drawing by Carpenter.

Fig. 10. Anterior view of metastoma of the trilobite *Triarthrus* from a drawing by Raymond.

#### Abbreviations.

**a**, Lobule of paragnath; **at**, Portion of basal segment of trilobitan limb homologized with second antenna; **b**, Lobule of paragnath; **bl**, basilamina, or basal lamina which bears the paragnath and maxillula; **bp**, Basiparagnath, or basal portion of paragnath; **c**, Epiparagnath, or appendage of paragnath; **dp**, Distiparagnath, or distal portion of paragnath; **li**, Lingua; **ll**, Lingualora, or lora of lingua; **md**, Mandibles; **mts**, Metastoma of trilobite; **mx**, First maxilla, or maxillula; **mxs**, Sternum of first maxillary segment; **pg**, Paragnaths, "superlinguæ", or "paragossæ"; **pc**, Pharyngocrista, or median pharyngeal ridge; **tc**, *Trophicostæ*, or rib-like structure at bases of trophi.

### PROCEEDINGS OF THE CAMBRIDGE ENTOMOLOGICAL CLUB.

At the meeting of February 8, Prof. W. M. Wheeler described the nesting habits of some ants of the genus *Carebara*, found in South America. These live in nests of Termites, making their own burrows between those of their hosts and feeding on the young of the latter. The various forms of these ants had been obtained from the stomachs of Anteaters killed near their nests. The males and females were of large size and the workers extremely small. When the males and females leave the nest for the mating flights some of these minute workers cling to their hairs, and when the females start new colonies these workers bring in food and feed the first-hatched young, which the female herself is unable to do.

Another genus of ants of small size, *Allomerus*, lives partly in the swollen branches of certain plants, going up and down between the plant and the underground nest in earth-covered galleries attached to the hairs of the plant.

Prof. C. T. Brues described some guests of Ants and Termites from South America. Wingless flies of the family *Phoridae* live in the nests of some ants and even travel with them in their raids outside the nest. In some termite nests are minute hymenopter-